

Contrasting perspectives on the measurements and taxonomy of *Arceuthobium* (Viscaceae): a long standing controversy

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ABSTRACT

Kuijt (2016) recently published an exceptionally critical, unsolicited review of two articles on the taxonomic classification of dwarf mistletoes (*Arceuthobium*, Viscaceae:) as well as the methods and morphological characters utilized to delimit taxa. We respond to the criticisms of our methods and conclusions as presented in a paper we recently published in *Phytologia* on the morphometric analysis of three species in sect. *Campylopoda*: *A. campylopodum*, *A. laricis*, and *A. tsugense*. Kuijt claimed that the foundation of our taxonomic conclusions for these taxa was primarily based on differences in the length of the third internode. This assertion is incorrect. The validity of these species was based on statistical inferences across multiple morphological characters from measurements of both male and female plants. Furthermore, Kuijt inferred that little information is currently available on the susceptibility of hosts to taxa in sect. *Campylopoda*. Again, we disagree and point out that there is a large body of literature demonstrating that there is host preference (i.e., host specificity) among the species of sect. *Campylopoda*—evidence that Kuijt has consistently ignored. The taxonomic classification he has proposed for sect. *Campylopoda* is equivalent to that available in the late 1800's. The implication is that no data relevant to the classification of this group has appeared for over 100 years! We summarized our position on the classification of sect. *Campylopoda* with supporting publications and point out the weaknesses in Kuijt's critique of our work. Research is never complete and additional data are always welcome, particularly from new molecular studies. However, at the present state of our knowledge we will continue to recognize the taxa in sect. *Campylopoda* as species—a classification used by most professional botanists and resource managers for over 40 years. Published on-line www.phytologia.org *Phytologia* 99(2): 95-110 (May 9, 2017). ISSN 030319430.

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Kuijt (2016) recently criticized the methods and conclusions of an investigation we published the previous year (Mathiasen and Kenaley 2015b) in which we reported additional morphological data for three taxa of *Arceuthobium* (Viscaceae) in sect. *Campylopoda*: *A. campylopodum* Engelm., *A. laricis* (Piper) St. John, and *A. tsugense* (Rosendahl) G.N. Jones. Because similar unsolicited reviews by the same author have appeared in other journals in the past, but gone unanswered (e.g. Kuijt 1973), we asked the editor of *Phytologia* to allow us to publish this response.

We need to first point out that Kuijt (2016) began his criticisms of our work with two disclaimers, noting that one taxonomic treatment of sect. *Campylopoda* is no better than another while acknowledging he himself is not an expert in morphometric analysis. Thereafter, he pivoted to a somewhat negative comment, “I shall accept at face value the authentic nature of the techniques employed and the data gathered, and focus on some serious flaws in the claimed *significance* of the mensural [sic] data.”

Because Kuijt admitted that he has no expertise in morphometric techniques and the application of modern statistical procedures, his assertion that there are errors in our methods and, hence, our results based on univariate and multivariate statistical analyses must be questioned immediately.

Instead of discussing in detail the many inconsistencies, ambiguous statements, and minor errors in the text of Kuijt's (2016) review of Mathiasen and Kenaley (2015b), we will first provide a brief overview of our past and present work on the taxonomic classification of *Arceuthobium* in sect. *Campylopoda* (for a detailed review see Mathiasen and Kenaley 2016) and, thereafter, focus on what we consider to be the key weaknesses of his criticisms. These include: 1) we do not emphasize nor base our taxonomic conclusions on differences in the length of the third internode of dwarf mistletoe plants; 2) although Kuijt argued that we cannot measure characters to the nearest 0.1 mm accurately, we and others can easily measure the morphological traits selected for comparison of populations to this level of precision using a variety of available equipment; 3) although our "taxonomic judgment" was questioned, we believe our judgment is as sound as the taxonomists who originally described the taxa under debate; 4) we did not emphasize variation in plant color as a major difference between the taxa we studied; and 5) although Kuijt maintained that there are no data available on differences in host susceptibility (i.e., indicative of host specialization) among the dwarf mistletoes we studied, in reality, there is a large amount of data on this subject which has been published and is available to the scientific community.

Taxonomic classification of *Arceuthobium*, section *Campylopoda*

The taxonomic classification of the taxa in sect. *Campylopoda* (*sensu* Hawksworth and Wiens 1972, 1996) has been under debate for many years, as Kuijt (2016) mentioned at the start of his critical review. In the last 20 years, several different classifications have been proposed for these ecologically and pathologically important parasitic plants (Hawksworth and Wiens 1996; Kuijt 2012; Nickrent 2012; Mathiasen and Kenaley 2015a; Nickrent 2016). Because these parasites are among the most serious pathogens of many commercially valuable conifers in Canada, Mexico, and the United States, agreement on a practical and stable taxonomic classification is critical for investigators currently addressing the systematics of this group. Although that may be a laudable goal, additional research, particularly using molecular approaches, will be necessary before it is likely to be achieved as *Arceuthobium* undoubtedly represents a taxonomically difficult genus. Extreme morphological reduction of leaves, flowers, and fruits has limited the morphological characters available for their comparison and study (Hawksworth and Wiens 1996).

Over the last decade, we have collected a large amount of additional morphological data and analyzed it using both univariate and multivariate statistics to provide further insights into the morphological differences among the taxa in sect. *Campylopoda*. In this same time, we have determined the morphological characters contributing most to species differences and, hence, species membership. We have now published several papers presenting our results which we interpreted as supportive of the classification of most of these taxa at the specific level (Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015a, 2015b, 2016; Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). This is the conclusion adopted by Hawksworth and Wiens (1972, 1996) and that which is followed by most professional foresters and forest pathologists in North America who deal with mitigating the damaging effects of these parasites in forest ecosystems (Hawksworth et al. 2002). All of our investigations not only reported statistically significant differences among the means of several morphological characters, but also reported differences in physiological characters (phenology and/or host specificity), which we maintained is further support for the classification of the taxa addressed as separate species or, in some cases, as subspecies. It goes without question that we emphasize the host range of dwarf mistletoes as a major factor in their classification and will continue to do so.

The Issue of Third Internode Length

With regard to Mathiasen and Kenaley (2015b), the major premise in Kuijt (2016) for asserting that our statistical analyses of morphological characters (plant heights, basal diameters, staminate spikes, and flower, fruit and seed dimensions) were all invalid was based solely on our measurement and reported results for the length of the third internode (LTI) among the largest male and female plants from each of the populations under study. His assertion that results related to LTI formed a “major structural part of the taxonomic conclusions” was incorrect. Although we reported LTI data, we never maintained that our taxonomic conclusions were based primarily on statistically significant differences in the mean LTI among taxa. For example, LTI was one of 18 morphological characters examined across female and male plants per population. Although we did indeed report that LTI strongly contributed to determining species membership when comparing female or male plants, we also clearly stated that other female and male morphologies — such as third internode width, seed and fruit length, staminate spike width as well as anther diameter and distance to tip — could be utilized separately or in combination to discriminate among *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*.

As illustrated in Figure 1 (Mathiasen and Kenaley 2015b), the multivariate means and associated 95% confidence ellipses for female (N= 8 characters) and male plants (N= 10 characters) for the aforementioned taxa do not intersect. Our discriminant function analyses clearly demonstrated that these three taxa are morphologically distinct and can be readily distinguished from each other using multiple characters. In addition, our ability to accurately predict species identified *a priori* in the field using only a few characters was exceedingly high (>90%). These three species are among the most morphologically distinct taxa in sect. *Campylopoda* and data on their host affinities also supported this conclusion (Hawksworth and Wiens 1996; Mathiasen and Kenaley 2015b). We are well aware of and will continue to address Kuijt’s concerns regarding the efficacy of using the LTI. For example, we have stated this fact in previous work (e.g., page 72 in Mathiasen and Daugherty 2013, page 380 in Mathiasen et al. 2016) and have explained several times our reasons for continuing to report third internode dimensions as well as including these measurements in our morphometric analyses of taxa in sect. *Campylopoda* (Mathiasen and Daugherty 2013; Mathiasen and Kenaley 2015a, 2015b, 2016; Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). Although we do not emphasize LTI as an informative morphological character in *Arceuthobium*, we have discussed in our publications that we believe the combination of comparing basal diameters and the width of the third internode (WTI) among populations is taxonomically informative in that it provided a meaningful comparison of the thickness of plant stems (Mathiasen and Daugherty 2013; Kenaley et al. 2016b; Mathiasen and Kenaley 2015a, 2016). Note that Mathiasen and Kenaley (2015b) summarized the principal characters separating *A. campylopodum*, *A. laricis*, and *A. tsugense* and included WTI, but not LTI (Table 1).

While we are willing to take into consideration Kuijt’s assertion that “Seasonal elongation of all internodes can be accepted as a fact in all large species of *Arceuthobium*” (Kuijt 1969), we would prefer to see specific data supporting this assumption rather than the extrapolation of his data from only male plants of *A. americanum* Nuttall ex Engelmann to all other large dwarf mistletoes. To the best of our knowledge, neither he nor other colleagues have reported these data; but we will continue to acknowledge that LTI should not be used as a principal character for the separation of *Arceuthobium* taxa. However, we will also continue to report measurements of this character so our results can be compared with Hawksworth and Wiens (1972, 1996) and with our other investigations to keep the historical record consistent.

Although Kuijt also claimed that we failed to mention the seasons or dates when measurements of third internode dimensions were conducted, these data can be obtained from voucher specimens of *Arceuthobium campylopodum* and *A. laricis* deposited at the Deaver Herbarium (ASC) and the University of Arizona Herbarium (ARIZ) via the public electronic database SEINet (SEINet 2016). Likewise,

voucher information for *A. tsugense* can be obtained from the herbarium at the Pacific Research Center, Canadian Department of Forestry, Victoria, British Columbia (DAVFP). Furthermore, we stated that flower measurements were obtained during the peak of flowering for male plants (primarily in August) and during the peak of seed dispersal for female plants (primarily in September) and, of course, this also indicated when all other plant measurements (plant heights, basal diameters, and third internode dimensions) were taken. All of this information is provided in the methods of our Phytologia paper (Mathiasen and Kenaley 2015b).

Accuracy of Measurements and Sampling Bias

As noted previously, Kuijt (2016) emphasized that because we report the mean LTI, this negates the taxonomic usefulness of other characters such as plant heights, basal diameters, and others that he did not define. We completely disagree with his contention and will continue to use these characters to compare dwarf mistletoe plants as others have done for nearly 40 years; see the literature cited in Hawksworth and Wiens (1996) and our publications cited here. Kuijt then implied that we cannot accurately measure morphological characters to the nearest 0.1 mm, an assertion we are sure plant taxonomists and other biologists must find indefensible. As do most investigators who are measuring and comparing small plant structures or microbes (e.g., glumes, lemmas, seeds, pollen, spores, etc.), we defined what equipment was used to measure morphological characters in all of our recent papers: a 7X ocular micrometer and a digital caliper — both of which easily allowed accurate and reproducible measurements to the nearest 0.1 mm. Why Kuijt (2016) finds reporting measurements to the nearest 0.1 mm “dubious” is unclear as he himself has reported morphological measurements for the fruits of several species of *Phoradendron* to the nearest 0.1 mm (e.g., see pages 86 and 96 in Kuijt 2003). Few biologists today would question the ability of investigators to measure morphological characters to the nearest 0.1 mm given the widespread use of ocular micrometers, digital calipers, and stereoscopes. There are many examples of morphometric analyses in the botanical literature and other fields in which investigators measured morphological characters of small plant structures to the nearest 0.1 mm (e.g. Harrison and Hebda 2011; Gardner et al. 2012). Mycologists and bacteriologists commonly measure spores and cells to the nearest 0.1 μm (e.g., Kenaley et al. 2016a). As most taxonomists fully realize, it is a common practice to report the size of morphological characters to the nearest 0.1 mm, or with even greater precision, for many organisms with small morphological characters.

We find Kuijt’s criticism regarding our method of measurement and sampling (Kuijt 2016) incongruous with his own approach to taxonomy as he did not report sample sizes, means, or standard deviations for any of the measurements of morphological characters throughout his monograph on *Phoradendron* (Kuijt 2003); yet, he criticized Nickrent (2012) for not reporting these statistics in the data Nickrent (op. cit.) used from Hawksworth and Wiens (1996) for LTIs. Since Nickrent cited Hawksworth and Wiens as the source of the third internode data, the sample sizes, means, ranges, and standard deviations for third internode measurements he used are accessible in Hawksworth and Wiens (1996, e.g., see page 199 for *Arceuthobium campylopodum*). It appears that Kuijt can hold us and colleagues to one set of standards while following another set that he deems appropriate for his work.

In the same paragraph in which Kuijt (2016) questioned our ability to measure characters accurately to the nearest 0.1 mm, he also criticized our use of flower morphology by maintaining that Nickrent (2012) stated that staminate flower width appeared to show little variation. Although we are unclear what connection there is to measuring staminate flower width to the nearest 0.1 mm and the aforementioned comment by Nickrent on flower width variation, we should point out that Nickrent (2012) relied on flower widths to separate many of the taxa he treats as subspecies of *Arceuthobium campylopodum* — taxa we treat as species. Furthermore, in his treatment of *Arceuthobium* in the Flora of North America, Nickrent (2016) also utilized flower width in his diagnostic descriptions. Evidently, Nickrent (2016) believed staminate flower diameters were consistent enough to use for separating taxa.

Again, we are confident that we, and other biologists, can accurately measure the size of the small flowers of dwarf mistletoes to the nearest 0.1 mm and, if we had chosen to do so, to even smaller precisions using microscopy and image capture technology (Cope et al. 2012). Furthermore, we have demonstrated using univariate and multivariate statistical analyses that mean staminate flower diameters were consistently and significantly different among many species in sect. *Campylopoda* (Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015a, 2015b; Reif et al. 2015; Kenaley et al. 2016b; Mathiasen et al. 2016). Claiming that because we measured the LTI negates the statistical significance of the other morphological characters we used to delimit taxa lacks merit.

Although Kuijt (2016) objected to our sampling of dominant (tallest) plants, we purposefully measured dominant plants on dwarf mistletoe-infected branches in order to standardize measurements of plants within and among populations. It would be meaningless to take a stratified sampling approach comparing the largest to the smallest plants among populations; doing so would require qualitative judgments on plant size(s) that would not be reproducible among populations (or investigators) and inherently would introduce sampling error. The maximum size of the largest plants we measured for *A. laricis* (9.8 cm, 32 populations) never reached the maximum lengths of plants of *A. tsugense*, (16.1 cm, 19 populations) and those of *A. tsugense* never reached the maximum heights observed for *A. campylopodum* (25.4 cm, 60 populations). By sampling and measuring hundreds of the largest plants, we can compare the relative plant size of each taxon over their geographic ranges. Plants must be compared among principal hosts as this is the “environment” in which the plants should reach their maximum growth potential. Thus, it would be meaningless as well to compare plants from less susceptible hosts, particularly rare hosts, as infections most often produce few or no plants. In addition, we always used the mean values for plant heights to detect significant variation among taxa using accepted statistical analysis methods (e.g., analysis of variance and multiple comparison procedures). One of the major reasons we chose to measure dominant plants on infected branches was because Hawksworth and Wiens (1972, 1996) also measured dominant plants for their morphological measurements; this maintained the ability for other investigators to replicate our work and that of Hawksworth and Wiens. Replication of research is dependent on using standardized methods that permit the comparison of results among or between studies. So while Kuijt asserted that the measurement of the dominant plants collected from principal hosts is inappropriate and that color differences are not useful because of environmental influences, we contend that these measurements, among others, provide the best means for standardizing comparisons across the geographic and host ranges of dwarf mistletoes.

The Taxonomic Judgment Paradigm

After criticizing our ability to measure morphological characters accurately, Kuijt (2016) next hypothesized that our measurements were accurate and that the differences among the taxa we compared in our 2015 Phytologia paper (*Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*) were consistent, thereby actually insinuating just the opposite perspective. He then asserted that these same consistent and statistically different morphological discontinuities did not support our conclusion that these taxa should be recognized as species. In support of his claim, Kuijt implied that our “taxonomic judgment” should be questioned on the basis that many living organisms cannot be easily classified using a Linnaean hierarchy. He cited two examples: gulls in the genus *Larus* that constitute what have been termed “ring species,” and the Caribbean slipper-spurge (*Euphorbia tithymaloides* L.) which may be an example of a plant that represents a “ring species.” Kuijt next stated that he does not believe that the taxa in sect. *Campylopoda* represent an example of a “ring species,” so we have not addressed that point in more detail. But why did he inject the concept of “ring species” if he did not believe it was plausible? Thereafter, and without any clear rationale, Kuijt stated that sect. *Campylopoda* could be an example of hybrid swarms (Nolte and Tautz 2010). However, the hybrid swarm analogy is moot when applied to sect. *Campylopoda* as the geographic ranges of many of the species in the section are isolated by hundreds of km and that some are reproductively isolated by differences in flowering period from the rest of the complex (e.g., *A.*

californicum Hawksworth & Wiens; Kenaley et al. 2016b). Even though the geographic ranges and flowering periods of several of the taxa in sect. *Campylopoda* do overlap, there is no published evidence that they hybridize (Hawksworth and Wiens 1972, 1996). However, Nickrent et al. (2004) and Nickrent (2012, 2016) maintained there is also no sound evidence that sympatric taxa in sect. *Campylopoda* do not hybridize. This question needs to be addressed; albeit challenging to prove or disprove sexual compatibility between the taxa (Mathiasen 1982). Thus, Kuijt (2016) ignored the opportunity to provide specific data or at least examples from the literature to support his assertion that taxa in sect. *Campylopoda* might be comparable to hybrid swarms in other plants; without such data and/or supporting literature his assertion that sect. *Campylopoda* taxa might represent hybrid swarms is baseless.

We must also clarify that we did not describe the three taxa in sect. *Campylopoda* examined in our article in Phytologia (Mathiasen and Kenaley 2015b). George Engelmann described *Arceuthobium campylopodum* in 1850 based on plant material collected from ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) from northeastern Washington state (see page 198 in Hawksworth and Wiens 1996). In 1903, R. O. Rosendahl was the first taxonomist to recognize that *A. tsugense* was distinct from *A. campylopodum* and classified it as a species under the genus *Razoumofskyia* Hoffman. In 1906, C. V. Piper was the first to recognize that *A. laricis* was morphologically distinct from *A. campylopodum* and warranted separate taxonomic recognition; but he classified it as a subspecies of *Razoumofskyia douglasii* (Engelmann) Kuntze. Gill (1935) acknowledged the host susceptibility differences exhibited by these dwarf mistletoes and treated both of these taxa as host forms of *A. campylopodum*: forma *laricis* (Piper) Gill infected western larch (*Larix occidentalis* Nuttall) and forma *tsugensis* (Rosendahl) Gill infected western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent)(and other hemlocks). In 1936, G. N. Jones rejected Gill's host-form concept and recombined *Razoumofskyia tsugensis* Rosendahl as *Arceuthobium tsugensis* as the 1930 Cambridge Botanical Congress voted to conserve *Arceuthobium* over *Razoumofskyia*. Thereafter, in 1937, H. St. John adopted the use of *Arceuthobium* over *Razoumofskyia* and recombined *A. laricis* as a species. Hawksworth and Wiens (1972, 1996) agreed with the classifications of these taxa as *A. tsugense* (not *tsugensis*) and *A. laricis*, summarized their nomenclatural history, and presented morphological, chemical, and host range differences among these taxa which further supported their classification at the specific level.

Our study of these taxa (Mathiasen and Kenaley 2015b) supplemented the morphological data presented by Hawksworth and Wiens (1972, 1996). Moreover, results of our statistical analyses supported the collective conclusions of Piper, St. John, Rosendahl, Jones, and Hawksworth and Wiens that the morphologies of *A. laricis* and *A. tsugense* were sufficiently distinct from *A. campylopodum* to be treated as species. Our investigation of these taxa was partly in response to Kuijt's continued insistence that these taxa, and others in sect. *Campylopoda*, should all be grouped under *A. campylopodum* (Kuijt 2012); a classification that we cannot accept. Furthermore, the vast majority of the professional publications related to *A. laricis* and *A. tsugense* in the last 40 years also recognized them as species (e.g., Smith et al. 1972; Taylor 1995; Beatty et al. 1997; Hennon et al. 2001; Muir and Hennon 2007); a fact demonstrating that resource managers in the United States and Canada who work with these dwarf mistletoes on a professional basis also accept their classification as species. Thus, when casting aspersions on our "taxonomic judgment," Kuijt (2016) also implied that all investigators over the last 110 years who have concluded that *A. laricis* and *A. tsugense* should be classified as distinct species suffer from the same lack of sound judgment. This includes not only the historically well-known plant taxonomists listed above but many other botanists who have classified additional taxa in sect. *Campylopoda* as species; this includes John Coulter, George Engelmann, Philip Munz, Aven Nelson, and Axel Rydberg (Hawksworth and Wiens 1996).

Kuijt's monograph for *Phoradendron* (Kuijt 2003) and his treatment of the Viscaceae for The Jepson Manual (Kuijt 2012) clearly indicated that he follows a typological species concept based mostly on the gross morphology of herbarium collections. The deficiencies of typological methodology have

been discussed by many biologists (Mayr 1963; Futuyma 1979; Yoon 2009). The idea dates back to Platonic philosophy and is predicated on a mind-set based on an idealized morphological “type” that places emphasis on the individual, not populations, with the result that variation tends to be either ignored or considered inconsequential (Minkoff 1983). We would add that ecophysiological specialization (host specialization), as well as geographic distributions and barriers to reproduction, are likewise considered to be of little importance in typological classifications. Such a concept abandons the Darwinian paradigm of population thinking and reproductive isolation that has withstood numerous attempts at falsification over the last 150 years (Minkoff 1983).

Plant Color

Although Kuijt (2016) criticized our mention of color differences between *A. campylopodum*, *A. laricis*, and *A. tsugense*, we discussed that only *A. laricis* had distinctively different colored plants (Mathiasen and Kenaley 2015b). However, we agree with Kuijt in general and have pointed out in several papers that plant color is usually an uninformative character for taxonomic classification of *Arceuthobium* (Mathiasen and Daugherty 2009b, 2013; Mathiasen and Kenaley 2015a; Mathiasen et al. 2016). Only when color differences are consistently and remarkably different have we commented on their value as a possible trait to distinguish between taxa (e.g. *A. littorum* Hawksworth, Wiens & Nickrent compared to *A. occidentale* Engelman; Mathiasen and Daugherty 2013, Mathiasen and Kenaley 2015a). Again, we would maintain that male and female plants of *A. laricis* often can be distinguished from *A. campylopodum* and *A. tsugense* based on color differences. Furthermore, we need to clarify that *A. laricis* is not the taxon occurring near the coast of Washington and British Columbia that Kuijt (2016) claims are greener; this would be a subspecies of *A. tsugense* discussed below.

Host Susceptibility

Kuijt (2016) claimed that we did not address in our Phytologia article (Mathiasen and Kenaley 2015b) the possibility of infrataxon variation in host susceptibility. However, we clearly discussed the major differences in host susceptibility among the three taxa we compared. Thus, to clarify, *Arceuthobium laricis* has not been observed to infect western hemlock (Mathiasen 1998). Mathiasen examined over 800 western hemlocks growing within 6 m of western larch severely-infected with *A. laricis* and found no infection on western hemlock. In addition, Smith (1974) attempted to artificially inoculate western hemlock with *A. laricis*, but no infections resulted. The relative susceptibility of different hosts to dwarf mistletoes is best assessed by quantifying infection on trees growing near severely-infected principal hosts because those trees are exposed to hundreds, if not thousands, of mistletoe seeds annually (Hawksworth and Wiens 1996). It has been demonstrated that one of the principal hosts of *A. campylopodum*, ponderosa pine, is only an occasional host of *A. laricis* (Hawksworth and Wiens 1996, Mathiasen 1998) (see page 43 in Hawksworth and Wiens 1996 for an explanation of the host susceptibility classification system used here: principal, secondary, occasional, and rare hosts). Mathiasen (1998) demonstrated the incidence of infection by *A. laricis* on over 750 ponderosa pines was 15% and plants of *A. laricis* maintained their morphological integrity when growing on this host. Infection of ponderosa pine is easily recognized as crossover infections by *A. laricis*; severe infection is obvious on western larch, while only a few ponderosa pines are infected and seldom are the pines severely-infected. The low level of infection of ponderosa pine by *A. laricis* has also been reported in Canada (Smith et al. 1972). In addition, Smith (1974) successfully inoculated ponderosa pine with *A. laricis*, and although only less than 1% of the seeds placed on trees resulted in infections, 100% of those infections produced aerial shoots. Because *A. tsugense* on western hemlock is not commonly sympatric with western larch there is currently no data on the natural susceptibility of western larch to this dwarf mistletoe (Mathiasen 1994; Hawksworth and Wiens 1996; Mathiasen and Daugherty 2005). However, Smith (1974) successfully inoculated western larch with *A. tsugense*, but only about 7% of the seeds used to inoculate trees produced infections and only 20% of the infections produced aerial shoots. It is

essentially impossible to extrapolate the results of artificial inoculations for estimating the relative susceptibility of western larch under natural conditions, but Smith demonstrated that western larch is susceptible to *A. tsugense* to some degree.

No data, of which we are aware, exist that demonstrate genetic differences among ponderosa pine severely infected by *Arceuthobium campylopodum* and those only occasionally infected by *A. laricis* in Oregon, Washington, and British Columbia. Arguing that the much lower level of infection observed and measured on ponderosa pine by *A. laricis* is merely intragenetic variation in host susceptibility of the pine has no merit based on the literature for either this dwarf mistletoe or ponderosa pine. There are no data on the susceptibility of western hemlock to *A. campylopodum* in nature because this tree species is not typically sympatric with ponderosa pine or Jeffrey pine (*Pinus jeffreyi* Greville & Balfour) — the principal hosts of *A. campylopodum*. However, Smith (1974) inoculated two western hemlocks with *A. campylopodum* (50 seeds on each tree) and found that none of the 100 seeds produced an infection. While inconclusive because of the small number of trees Smith inoculated, his research suggested that western hemlock is probably immune to infection by *A. campylopodum*. The apparent immunity of western hemlock to *A. campylopodum* (*sensu stricto*) clearly does not support Kuijt's continued argument that *A. tsugense* and *A. campylopodum* are the same species. However, there is certainly evidence that there is considerable variation in the susceptibility of ponderosa pine and Jeffrey pine to *A. campylopodum* (Scharpf and Roth 1992; Scharpf et al. 1992) and western hemlock to *A. tsugense* (Smith et al. 1993); this variation is the basis for identifying potentially resistant trees to dwarf mistletoes, as well as other plant pathogens.

The fact that Kuijt does not consider host susceptibility differences important is exemplified by his statement “I do not seriously believe host species *per se* make much of a difference, except perhaps sometimes in vigor” (page 6 in Kuijt 2003, and see his discussion of the unimportance of hosts on pages 30-33). Hence, Kuijt has continually ignored much of the scientific literature demonstrating host preference(s) of taxa in sect. *Campylopoda* and continues to do so. It is evident from his arguments that he does not fully understand the contributing factors and processes influencing host-specialization (Kuijt 2003, 2016). The scientific literature is full of examples that have clearly demonstrated the interconnection between host-specific obligate parasites and their hosts (Flor 1971; Brooks and McLennan 1993; Dybadhl and Storfer 2003; Little et al. 2006) including mistletoes (Norton and Carpenter 1998), as well as the factors driving diversification in host-parasite complexes (Barrett et al. 2008). The concept of the host range for a plant pathogen, which includes parasitic plants, is well-accepted in the field of plant pathology and is often applied as a central criterion for species/subspecific delineation of phytopathogenic organisms as “host switching” influences the evolutionary trajectory of the pathogen (Hoberg and Brooks 2008). Not considering the relationships between hosts and mistletoes in the taxonomic classification of the latter, is analogous to ignoring the specialization many plants exhibit for growth on serpentine soils (serpentine indicators/endemics) and the taxonomic classification of those plants as species or subspecies primarily based on their affinity to serpentine (Kruckeberg 1984, Alexander et al. 2007).

Kuijt's (2016) argument asserting that host susceptibility could influence morphological data was based on one photo (Figure 10 in Kuijt 1955) illustrating crossover infections on white spruce (*Picea glauca* (Moench) Voss), a rare host of *Arceuthobium americanum*. The photo illustrated a situation where one white spruce was severely infected whereas another white spruce growing in close proximity was not infected. His argument was unconvincing because this pattern of infection is commonly observed on rare host-dwarf mistletoe combinations. Severe infection of a few white spruce by *A. americanum* with little or no infection of other white spruce growing nearby severely-infected trees has also been reported by Baranyay (1970) and Smith et al. (1972). We have also seen examples of this “all or nothing” infection pattern for other rare hosts of dwarf mistletoes. Thus, there is no “absence of data” as Kuijt (2016) claims on the susceptibility of various hosts to *A. tsugense* (Smith 1971, 1974; Mathiasen 1994; Hawksworth and

Wiens 1996; Mathiasen and Daugherty 2005) and *A. laricis* (Smith 1971, 1974; Hawksworth and Wiens 1996; Mathiasen 1998), but we acknowledge that additional data are needed on the relative susceptibility of several hard pines to *A. campylopodum* (Mathiasen and Kenaley 2015a). However, we have previously observed *A. campylopodum* in mixed ponderosa pine-western larch stands numerous times in Oregon and Washington and, to date, have yet to find a single infection by *A. campylopodum* on western larch. We certainly need quantitative data to support these observations; however, it appears that western larch is immune to infection by *A. campylopodum* in those areas.

We cannot emphasize enough the importance for resource managers to have a taxonomic classification available for *Arceuthobium* that embraces the major differences in host susceptibility that have been observed and/or quantified. Dwarf mistletoe infection has been demonstrated unequivocally to be associated with significant growth losses and premature mortality of severely infected hosts (Hawksworth and Wiens 1996; Hawksworth et al. 2002). Foresters managing dwarf mistletoe populations to mitigate their damaging effects often apply a “species selection” management strategy in mixed-conifer forests infested with one or more dwarf mistletoes. This management approach applies existing knowledge of host susceptibilities to different species of *Arceuthobium* to assist in the execution of forestry operations that shift long-term species composition of infested stands to less susceptible and/or immune conifers. Classifying all of the species we recognize in sect. *Campylopoda* as *A. campylopodum* would mean that nearly all of the trees in each genus in the Pinaceae, except *Pseudotsuga* Carrière, would be a principal host of *A. campylopodum*. Given our own experience and appreciation of the literature demonstrating host affinities in *Arceuthobium*, we currently only consider hard pines to be the principal hosts of *A. campylopodum* (*sensu stricto*) and one of these principal hosts, ponderosa pine, is immune to eight of the species we recognize in sect. *Campylopoda* (Hawksworth and Wiens 1996). Classifying all dwarf mistletoe in sect. *Campylopoda* as *A. campylopodum* would severely hamper the use of “species selection” for the management of these dwarf mistletoes in the western United States and Canada; foresters would be unable to use our knowledge of host susceptibility and grow less susceptible conifers where and when appropriate. We realize that Kuijt is not concerned with this issue, but we know for certain that foresters and forest pathologists routinely apply host distribution(s) in their design and execution of dwarf mistletoe control operations. Thus, resource managers must have a taxonomic system for *Arceuthobium* that acknowledges the host susceptibility differences that have been reported by numerous investigators for over 100 years (Hawksworth and Wiens 1996; Mathiasen and Kenaley 2016).

The populations of *A. tsugense* that Kuijt (2016) discussed parasitizing *Pinus contorta* Douglas ex Loudon in the coastal areas of British Columbia are what most botanists and foresters classify as shore pine (*P. contorta* subsp. *contorta*; Critchfield and Little 1966, Price et al. 1998). These mistletoe populations parasitizing shore pine as a principal host have been classified as *A. tsugense* subsp. *contortae* Wass & Mathiasen (Wass and Mathiasen 2003). The pine often parasitized by *A. laricis* in the interior of southern British Columbia is a subspecies (or sometimes treated as a variety) of lodgepole pine (Rocky Mountain lodgepole pine, *P. contorta* subsp. *latifolia* (Engelmann) Critchfield) which is classified as a secondary host of *A. laricis* (Hawksworth and Wiens 1996, Mathiasen 1998). Although Kuijt considered the classification of *A. tsugense* subsp. *contortae* as “dubious,” the distinctiveness of subsp. *contortae* has long been recognized (Smith 1971, 1974; Smith and Wass 1976, 1979; Wass 1976). The dwarf mistletoe on shore pine in southern British Columbia was considered a host specific race of *A. tsugense* for many years (Hawksworth 1987; Hawksworth and Wiens 1996). However, Wass and Mathiasen (2003) classified it as a subspecies based on morphological discontinuities and, particularly, phenological as well as host range differences. Western hemlock is only an occasional host of *A. tsugense* subsp. *contortae* and this level of susceptibility has been clearly documented by Smith and Wass (1976), Wass (1976), and Wass and Mathiasen (2003). Therefore, Kuijt’s assertion that both *A. tsugense* and *A. laricis* “not uncommonly parasitizes *Pinus contorta* Dougl. ex Loud., on which it also can perpetuate itself (in at least some coastal locations, surely for many hundreds of years)” is misleading in that he was actually referring to what we consider as two different dwarf mistletoes and botanists specializing on the genus *Pinus*

consider two taxonomically different subspecies of *P. contorta*. Kuijt then asked “The pivotal question is: can we distinguish plants in these two different occurrences on *P. contorta*?” The answer to his question is definitively, yes. We can distinguish between *A. tsugense* subsp. *contortae* plants growing on the coastal subspecies of lodgepole pine (shore pine) from those of the morphologically distinct *A. laricis* parasitizing Rocky Mountain lodgepole pine in the interior of British Columbia (Mathiasen and Kenaley 2015b).

Another important counterpoint to note relative to Kuijt’s (2016) assertion that morphological data should be collected from non-principal hosts in order to provide convincing evidence for the recognition of infraspecific taxa in sect. *Campylopoda* is that several taxa in this group only parasitize one host. For example, *Arceuthobium abietinum* Engelman ex Munz f. sp. *magnificae* Hawksworth & Wiens, and *A. californicum* only infect red fir (*Abies magnifica* A. Murray) and sugar pine (*Pinus lambertiana* Douglas), respectively; whereas, *A. apachecum* Hawksworth & Wiens and *A. blumeri* A. Nelson parasitize only southwestern white pine (*Pinus strobiformis* Engelman) (Hawksworth and Wiens 1996; Kenaley et al. 2016b). Therefore, species of *Arceuthobium* with strictly one principal host precludes the opportunity to make morphological measurements on less susceptible hosts (secondary, occasional, or rare). Furthermore, plants on occasional and certainly rare hosts would not be comparable to plants on principal hosts. Therefore, we will continue to standardize our measurements of dominant plants from only principal hosts for morphological comparisons. However, our studies have already demonstrated some small differences between plant heights on principal hosts and occasional hosts (Mathiasen and Daugherty 2013; Mathiasen et al. 2016), but for some taxa we have found no significant differences between plant heights on different principal hosts (Mathiasen 2011, Mathiasen and Kenaley 2015a). Nevertheless, for the same species of *Arceuthobium*, other characters such as flower dimensions, staminate spike dimensions, and fruit/seed dimensions do not differ significantly on different principal hosts. We believe that the standardization of using the dominant plants for morphological comparisons among principal hosts is the most appropriate methodology, permitting replication of results which can then be cited as supporting or refuting our taxonomic conclusions. Using plants from occasional and rare hosts would bias the results because dwarf mistletoes frequently form few plants on these hosts. However, plants formed on secondary hosts may be acceptable for taxonomic comparisons and this idea deserves further study.

CONCLUSIONS

We have acknowledged Kuijt’s concerns regarding the use of the LTI in support of the classification of taxa in sect. *Campylopoda* (Mathiasen and Daugherty 2013; Mathiasen et al. 2016). Although we have not emphasized LTI to reach taxonomic conclusions, contrary to what Kuijt claimed (Kuijt 2016), we will continue to measure and report third internode dimensions (length and width) because these characters have been reported for dwarf mistletoe since the 1970s (Hawksworth and Wiens 1972) and provide some taxonomic information for comparing different populations of dwarf mistletoes. However, we have not, nor will we ever, base our taxonomic conclusions solely on LTI.

We do not agree with Kuijt’s conclusion that no infraspecific classification for sect. *Campylopoda* may be acceptable. The classification of this group by Hawksworth and Wiens (1996), with the addition of a few new subspecies (Wass and Mathiasen 2003; Mathiasen and Daugherty 2007, 2009a; Scott and Mathiasen 2009), has provided a practical and easily applied classification which considers morphological, phenological, and, most importantly, host affinities. Hawksworth and Wiens’ classification system has been accepted and is presently used by most professional foresters, forest pathologists, and many botanists who manage these economically and ecologically important parasitic flowering plants.

Adopting a taxonomic classification for sect. *Campylopoda* that does not recognize infraspecific taxa, neither reflects nor advances the totality of knowledge presently available for the designation of species in this group. Kuijt's classification of sect. *Campylopoda* is essentially a classification that sets the taxonomy of this group back to the late 1800s (Kuijt 2012) and is even more unacceptable and impractical than the host-form concept Gill (1935) proposed (Mathiasen and Kenaley 2015a). While we do not agree with Nickrent's (2012, 2016) treatment of most taxa in sect. *Campylopoda* as subspecies of *A. campylopodum*, it is a better approach to this group than that proposed by Kuijt (Kuijt 2012). We believe there are many problems with Nickrent's interpretation regarding the importance of morphological differences and host affinities for classification of dwarf mistletoes, but the principal issues are related to his classification of *A. abietinum*, *A. blumeri*, *A. microcarpum* (Engelmann) Hawksworth & Wiens, and *A. tsugense* as subspecies of *A. campylopodum*. His classification completely obscures the fact that there are cryptic taxa described as subspecies under *A. abietinum*, *A. microcarpum*, and *A. tsugense* (Hawksworth et al. 1992; Wass and Mathiasen 2003; Mathiasen and Daugherty 2007, 2009a; Scott and Mathiasen 2009). Furthermore, we and colleagues, including Nickrent himself, have demonstrated that *A. blumeri* is morphologically and genetically distinct from other dwarf mistletoes that parasitize white pines as well as *A. campylopodum* (Mathiasen 1982, Hawksworth and Wiens 1972, 1996; Nickrent et al. 2004; Reif et al. 2015; Kenaley et al. 2016b). Therefore, we will continue to support the classification of these taxa as species as well as recognize the subspecies that have been delineated under *A. abietinum*, *A. microcarpum*, and *A. tsugense* (e.g. *A. tsugense* subsp. *contortae*). Furthermore, we recommend that botanists, forest pathologists, and foresters continue to apply the Hawksworth and Wiens (1996) classification to dwarf mistletoes as it is the most practical and useful treatment for the management, and when appropriate, conservation of dwarf mistletoes (Mathiasen and Kenaley 2016).

Finally, we cannot agree with Kuijt's (2016) conclusion that "It is advisable to avoid infraspecific categories until the relevant variation patterns of both parasites and hosts are better known, as such categories tend to reflect a deceptive sense of accuracy." Most of the species that have been described in sect. *Campylopoda* were delineated in the late 1800s and early 1900s, over 100 years ago. Additional species and subspecies were described in the late 1960s (Hawksworth and Wiens 1972, 1996). All of these taxa have been accepted by the large majority of resource managers that work with these parasitic plants. There is now a large amount of data relevant to the morphological, phenological, and host range variation for all of the dwarf mistletoes in sect. *Campylopoda*. However, more data are certainly needed, particularly molecular information related to the population genetics of dwarf mistletoes and their hosts. Such open-ended statements as in the first sentence above, obviously leaves us asking exactly what are the relevant variation patterns and how much do we need to know about them before anyone can propose an alternative classification to Kuijt's for sect. *Campylopoda*? Kuijt would have us remain stagnant using a classification dating from the late 1800s instead of synthesizing new morphological and molecular data collected with modern methods and technologies to continually update and improve the classification of *Arceuthobium* in the 21st century and beyond. We prefer to move ahead instead of living in the 19th century with Kuijt.

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Table 1. Summary of the principal characters separating *Arceuthobium campylopodum*, *A. tsugense*, and *A. laricis*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers in bold represent key morphological or phenological differences between the taxa. Host susceptibility classification based on information in Hawksworth (1987), Hawksworth and Wiens (1996), Mathiasen (1998), and Mathiasen and Daugherty (2005, 2007). This is Table 2 in Mathiasen and Kenaley (2015b).

Character	<i>Arceuthobium campylopodum</i>	<i>Arceuthobium laricis</i>	<i>Arceuthobium tsugense</i>
Plant height			
Female	10.4	5.3	8
Male	9.7	4.7	7.8
Plant color	Yellow-green, green, yellow-brown	Brown-green, red, purple	Yellow-green, green, yellow-brown
Basal diameter			
Female	3.4	2.4	2.7
Male	3.2	2.1	2.6
Third internode width			
Female	2.5	1.7	1.6
Male	2.5	1.7	1.6
Staminate spike width	3.1	2.6	1.6
Flower diameter			
3-merous	3.1	2.7	3.2
4-merous	4.2	3.7	3.8
Fruit length	5.4	4.3	4.4
Fruit width	3.7	3	2.9
Sympatry among taxa	<i>A. laricis</i>	<i>A. campylopodum</i>	Not sympatric
Host Susceptibility			
Principal	<i>Pinus jeffreyi</i> ; <i>P. ponderosa</i>	<i>Larix occidentalis</i>	<i>Tsuga heterophylla</i>
Secondary	<i>P. attenuata</i> ; <i>P. coulteri</i>	<i>Tsuga mertensiana</i> ; <i>P. contorta</i> var. <i>latifolia</i>	None
Occasional	<i>P. contorta</i> var. <i>murrayana</i> , var. <i>latifolia</i> ; <i>P. sabiniana</i>	<i>Abies lasiocarpa</i> ; <i>Pinus ponderosa</i>	<i>Abies amabilis</i> ; <i>A. grandis</i> ; <i>A. procera</i> ; <i>Pinus contorta</i> var. <i>latifolia</i> ; <i>Tsuga</i> <i>mertensiana</i>
Rare	<i>P. lambertiana</i>	<i>Abies grandis</i> ; <i>Picea</i> <i>engelmannii</i> ; <i>Pinus</i> <i>albicaulis</i> ; <i>P.</i> <i>monticola</i> ; <i>Tsuga</i> <i>heterophylla</i>	<i>Picea engelmannii</i> ; <i>P.</i> <i>sitchensis</i> ; <i>Pinus monticola</i> ; <i>Pseudotsuga menziesii</i>
Immune	<i>Abies grandis</i>		<i>P. contorta</i> var. <i>murrayana</i>

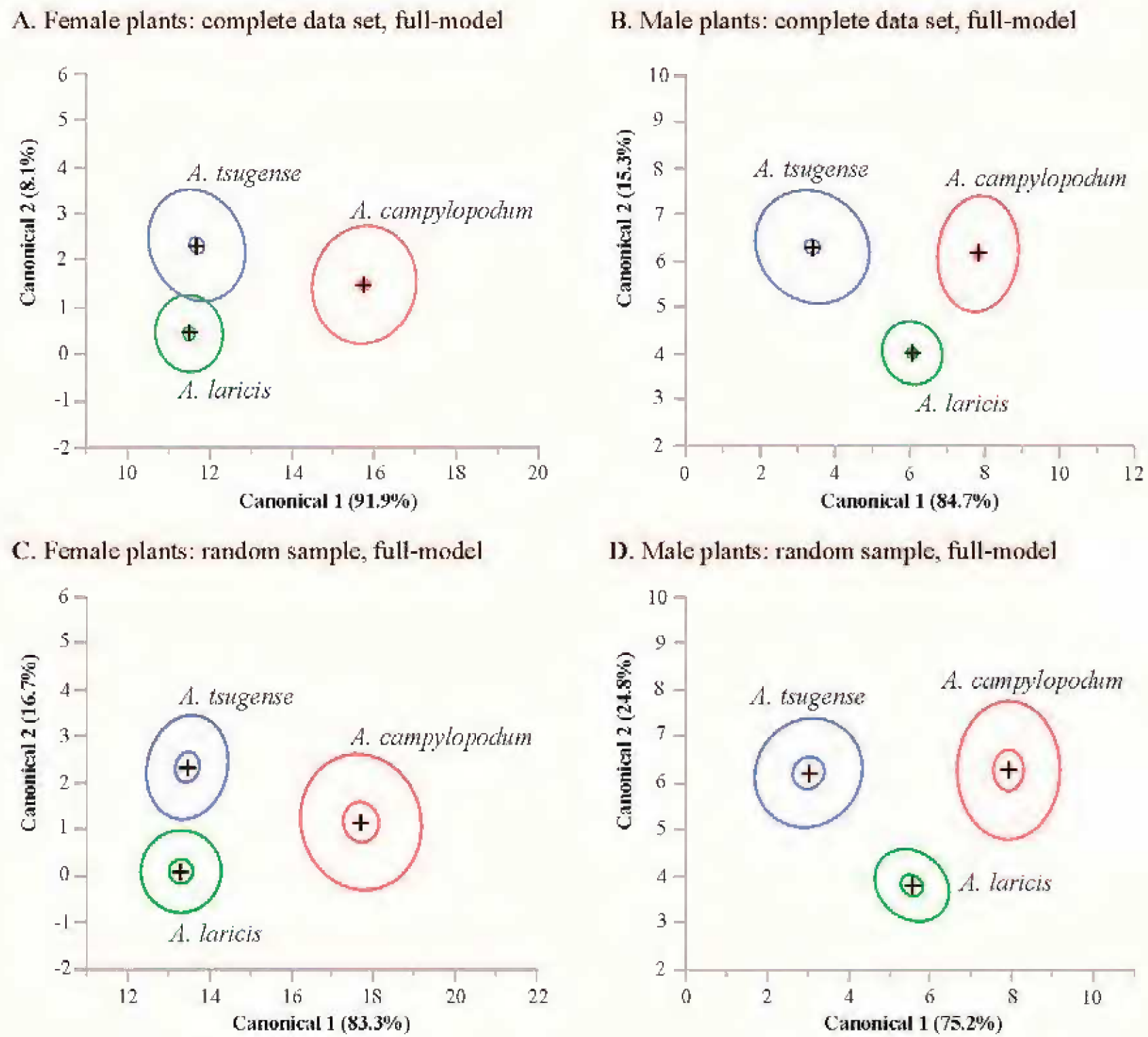


Figure 1. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 6. Multivariate means (squares) were computed using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using a random subset (50 complete records/species) of female (C) and male plants (D), respectively. For each species (A-D), the inner ellipse correspond to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within which 50% of plants for each species reside. From Mathiasen and Kenaley (2015b).